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# The role of the motor system in action imagination and comprehension

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## ABSTRACT

Covert actions encompass cognitive processes such as motor imagery, action observation, and action language. These processes ignite motor simulations within the mind and engage neural circuits underlying sensorimotor functions, offering promising potential for optimizing motor performance and rehabilitation strategies. Yet, despite broad consensus on the motor system's involvement, its precise role — whether a dynamic embodiment mechanism or a mere epiphenomenon — remains a matter of intense debate. In this review, we present a comprehensive analysis of motor system engagement across motor imagery, action observation, and action language. First, we examine correlational evidence derived from functional magnetic resonance imaging and transcranial magnetic stimulation studies in healthy individuals, including those with impaired mental simulation abilities. This evidence helps elucidate whether, and to what extent, these cognitive processes recruit the motor system, particularly the primary motor cortex. We then turn to causal evidence, which allows us to infer the functional role of the motor system in these processes. Specifically, we review findings from studies investigating behavioral changes, patients with lesions, and artificial lesions in healthy participants created using neuromodulation techniques. By integrating these perspectives, we seek to clarify this ongoing debate by illuminating the functional role of the motor system in motor imagery, action observation, and action language.

## 1. Introduction

The ability to imagine and understand actions constitutes an extraordinary capacity of Humans. This encompasses so-called covert actions, which particularly refer to motor imagery, action observation and action language understanding. Motor imagery corresponds to the explicit mental simulation of an action, without concomitant movements. The two most common modalities to imagine a movement are visual and kinesthetic. One can visually experience the action (visual modality) from a first- or third-person perspective and/or recreate the articular and muscular sensations associated with a specific movement (kinesthetic modality). In contrast, action comprehension is an implicit process (when no instruction is given to explicitly use motor imagery), which involves either watching someone moving, known as action observation, or reading and listening about described actions, known as action language. When studying such covert actions, it is important that participants remain at rest so as to specifically isolate neural activation

associated with these mental processes, while excluding that of action execution. Numerous researchers have suggested that the motor system — a cortical and subcortical network associated with movement planning, initiation and execution — is involved when we imagine actions (Grosprêtre et al., 2016b; Lotze et al., 1999; Miller et al., 2010), observe an action being performed (Dushanova and Donoghue, 2010; Fadiga et al., 1995; Kilner and Frith, 2007; Naish et al., 2014) and read about actions (Aziz-Zadeh et al., 2006; Dupont et al., 2024a; Hauk et al., 2004). However, the genuine utility of the motor system activation during such processes remains a heavily debated topic, with considerable skepticism regarding the contribution of the primary motor cortex (M1) during action imagining and understanding (Mahon, 2020, 2015; Mahon and Caramazza, 2008; Wurm and Caramazza, 2019). For instance, using an fMRI method that distinguishes different laminar contributions, a recent study by Persichetti et al. (2020) found that while overt motor actions activated both superficial and deep cortical layers in M1, motor imagery engaged only the superficial layers. According to

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this result, M1 activation during motor imagery might be merely epiphenomenal. However, other neurophysiological findings support the idea that the activation of the motor system during these covert actions is not restricted to M1 and goes beyond the superficial layers of M1 (Dupont et al., 2025a,b,c; Grosprêtre et al., 2019, 2016a). Unravelling whether the motor system is functionally involved in covert actions addresses a fundamental question in the field of embodied or situated cognition. It is possible that motor system engagement is necessary for thinking about actions (remembering, understanding, planning, etc.). If covert actions indeed engage the motor system in a functional manner, not only would this respond to a fundamental question in cognitive neuroscience, but it would also provide a springboard for practical applications. For instance, evidence for this idea would hold significant promise for improving motor performance in two domains where even the slightest improvements can have a critical impact: high-level sports and clinical rehabilitation.

The current review delves into this current debate, summarizing both correlational and causal evidence regarding the role of the motor system, particularly M1, in covert actions, such as imagining, observing, and reading actions. Grasping both types of evidence is essential, as correlational evidence serves to pinpoint the patterns of activity underlying covert actions, while causal evidence reveals the role played by the motor system in these processes. First, we review correlational evidence derived from neuroimaging and transcranial magnetic stimulation (TMS) studies in healthy subjects, including those with impaired imagery (aphantasia). Then, we explore causal evidence from studies focusing on behavioral changes, functional lesions, and virtual lesions induced by neuromodulation techniques. This comprehensive and narrative review clarifies the role of the motor system in covert action processes.

## 2. Motor system in covert actions: correlational evidence

### 2.1. Correlational evidence from imaging studies

The functional Magnetic Resonance Imagery (fMRI) and Positron Emission Tomography (PET) techniques provide information on the level of blood oxygenation circulating in brain areas during perceptual, motor and cognitive tasks, indirectly revealing the activation of the neural network. Over several decades, these methodologies have helped to develop an extensive literature on the specific cerebral networks activated during motor imagery, action observation and action reading.

#### 2.1.1. Motor imagery

Motor imagery engages a large fronto-parietal network, including bilateral activation of the frontal and precentral gyrus in the frontal lobe (Hardwick et al., 2018; Héту et al., 2013; Lotze et al., 1999; Van Cae-negem et al., 2024), as well as bilateral activation of the postcentral gyrus, superior parietal lobule, and inferior parietal lobule in the parietal lobe (Fleming et al., 2010; Gerardin et al., 2000; Lacourse et al., 2005; Lebon et al., 2018; Porro et al., 1996; Sharma and Baron, 2013). In addition, subcortical structures, such as the right thalamus, the basal ganglia, and the cerebellum, are at play during motor imagery (Habas and Manto, 2014; Hanakawa et al., 2003; Hardwick et al., 2018; Héту et al., 2013; Lotze et al., 1999; Ryding et al., 1993; Szameitat et al., 2007). Hanakawa et al. (2003) observed posterolateral cerebellar activations, potentially corresponding to lobules VI, VII, VIII, crus I, during both motor imagery and action execution, while the anterior cerebellum was activated only during action execution.

Although this cortical and subcortical network remains relatively constant during motor imagery, it may vary according to several factors such as the effector involved in the imagined movement (e.g., hand vs. foot; Héту et al., 2013), the motor imagery modality (e.g., visual vs. kinesthetic, Binkofski et al., 2000; Guillot et al., 2009a,b; Héту et al., 2013; Solodkin et al., 2004), the motor imagery skill (poor vs. good imagers; Guillot et al., 2008; Lafleur et al., 2002) and motor expertise

(novice vs. expert; Chang et al., 2011; Milton et al., 2008).

In summary, the supplementary motor and premotor cortices are thought to coordinate the preparation, planning and control of motor simulations while preventing overt movement during motor imagery (Guillot et al., 2014; Hardwick et al., 2018; Kasess et al., 2008). The parietal lobe likely generates, sustains, and refines these motor simulations (Guillot et al., 2014). Finally, the cerebellum may anticipate the sensorimotor consequences of imagined actions (Rannaud Monany et al., 2022a).

#### 2.1.2. Action observation

Action observation recruits brain regions that are part of the motor and mirror neuron systems, extending from fronto-parietal to occipito-temporal regions (Courson and Tremblay, 2020; Hardwick et al., 2018). Similar to motor imagery, action observation recruits inferior and middle frontal gyrus (Caspers et al., 2010; Grèzes and Decety, 2000; Iacoboni et al., 2005; Johnson-Frey et al., 2003; Molnar-Szakacs et al., 2005; Simone et al., 2017), superior and inferior parietal lobules (Buccino et al., 2001; Grèzes and Decety, 2000; Urgen et al., 2019), as well as postcentral gyrus (Blakemore et al., 2005; Gazzola and Keysers, 2009; Keysers et al., 2004). In addition, action observation activates the visual cortex, notably the right extrastriate visual cortex during the observation of biological motion (Caspers et al., 2010; Hardwick et al., 2018; Vaina et al., 2001).

Action observation, in contrast to motor imagery, raises a deeper controversy concerning the activation of subcortical structures. Some authors do not report any activation of the cerebellum (Nedelko et al., 2012; Taube et al., 2015), whereas others do (Abdelgabar et al., 2019; Calvo-Merino et al., 2006; Errante and Fogassi, 2020; Frey and Gerry, 2006; Molenberghs et al., 2012). For example, Errante and Fogassi (2020) recently showed bilateral activation of cerebellar lobule V, VI, crus I, VIIa and VIIb during the execution and observation of object manipulation with the right hand, overlapping with the neural patterns of motor imagery. In addition, there is recent evidence for activation of the left putamen and thalamus (Courson and Tremblay, 2020; Ge et al., 2018; Hardwick et al., 2018).

Therefore, action observation involves a wide cortical network (and sub-cortical, although still under debate), where each system seems to play a distinct role (Urgen et al., 2019). The occipito-temporal cortex may be involved in visual analysis of actions integrating shape and movement information, whereas parietal cortex would rely on these visual representations and would create more abstract and semantic representations encoding the action target, action type, and intention (Desmurget et al., 2009; Desmurget and Sirigu, 2012). Then, the pre-motor cortex may convert them into a motor code for understanding how the action is physically performed (Urgen et al., 2019). Finally, the cerebellum cortex would likely be involved in predicting sensorimotor consequences during action observation, as suggested during motor imagery (Errante and Fogassi, 2020).

#### 2.1.3. Action reading

Action reading also relies on a large distributed network including fronto-parietal and temporo-occipital regions. Concerning the frontal lobe, action reading solicits the frontal and precentral gyrus (Courson and Tremblay, 2020; Hauk et al., 2004; Pulvermüller, 2005; Tettamanti et al., 2005) with minor variations depending on the action word effector. Although the superior frontal gyrus is activated during passive reading of general action words, Hauk et al. (2004) observed activation in the middle frontal gyrus for hand and arm action words, while the inferior frontal gyrus was recruited for facial action words. This study also reported somatotopic activation for action words within the pre-central gyrus (M1, see also, Aziz-Zadeh et al., 2006; Tettamanti et al., 2005; Wu et al., 2013).

Reading comprehension in general elicits an activation of the left inferior parietal lobule (Binder et al., 2009; Javed and Wroten, 2018; Seghier, 2013; Vandenberghe et al., 1996), and the left temporal gyrus,

especially the superior portion (Achal et al., 2016; Courson and Tremblay, 2020; Jobard et al., 2003; Tyler et al., 2003). As previously mentioned, action reading recruits the occipital and primary visual cortices. Similar to action observation, the extrastriate visual cortex is also recruited for visual perception and interpretation during reading (Aziz-Zadeh et al., 2006; Planton and Démonet, 2012; Willems et al., 2010; Yang and Shu, 2014).

Reading in general, and therefore reading about actions, recruits subcortical structures. The cerebellum activation is more widely reported (Brignoni-Perez et al., 2020; Carota et al., 2012; Fiez and Petersen, 1998; Li et al., 2021; Mariën et al., 2014; Yang and Shu, 2014) compared to the basal ganglia (Carota et al., 2012; Oberhuber et al., 2013; Price et al., 1994), or the thalamus (Price et al., 1994; Yang and Shu, 2014). For example, Carota et al. (2012) asked participants to read tool words referring to a hand action and reported activation in cerebellar lobules V, VI, VIII, crus I, with subtle variations depending on the type of word being processed. Interestingly, the recruitment of these lobules during reading appears to overlap, at least partially, with neural patterns observed during motor imagery and action observation.

In summary, when reading words in general, the occipito-temporal network is involved in visual information processing, letter and word recognition, and prelexical analysis, while the inferior frontal cortex plays a central role in semantic processing (Binder et al., 2009; Dehaene et al., 2002; Dehaene and Cohen, 2011; Perrone-Bertolotti et al., 2014; Vigneau et al., 2006). When words describe an action, the premotor and primary motor cortices may facilitate semantic access by linking linguistic input to motor simulations, thereby enhancing action comprehension. Finally, while the role of the cerebellar cortex during reading in general as well as action reading remains debated, evidence suggests that its contribution extends beyond motor articulation to encompass high-level, non-motor linguistic functions, including language comprehension (Mariën et al., 2014).

#### 2.1.4. Primary motor cortex activation during motor imagery, action observation and action reading

Despite the activation of the motor network during motor imagery, the involvement of M1 is still debated (for reviews, see: Héту et al., 2013; Madan and Singhal, 2012; Munzert et al., 2009). For instance, some authors report M1 activation during the imagination of hand movements (Ehrsson et al., 2003; Hallett et al., 1994; Lotze et al., 1999; Schnitzler et al., 1997; for intracranial evidence, see Miller et al., 2010), finger-/thumb sequences (Nair et al., 2003; Porro et al., 1996; Sharma et al., 2008) or toe/foot movements (Ehrsson et al., 2003; Stippich et al., 2002), whereas other studies do not report any activation, or only activation of superficial layers (Courson and Tremblay, 2020; Gerardin et al., 2000; Hanakawa et al., 2003; Kuhtz-Buschbeck et al., 2003; Persichetti et al., 2020). Interestingly, the same controversy exists for action observation and action reading. Indeed, M1 activation during action observation is generally not reported in humans when using fMRI (Courson and Tremblay, 2020; Hardwick et al., 2018; Taube et al., 2015). Nonetheless, intracranial recordings in non-human primates have demonstrated that action observation of arm movements in a target pursuit task (Tkach et al., 2007) or target reaching task (Dushanova and Donoghue, 2010) leads to an activation of M1 neurons. More specifically, subsets of pyramidal neurons within the premotor and primary motor cortices of macaque monkeys have been reported to exhibit classical mirror-like properties — i.e., increased activity during both execution and observation of action. Interestingly, another population of M1 pyramidal neurons has been described as reversed or suppression mirror-neurons, characterized by reduced activity only during action observation (Jerjian et al., 2020; Kraskov et al., 2009, 2014; Vigneswaran et al., 2013). These studies provide neurophysiological evidence that M1 is activated during action observation, involving both facilitatory and inhibitory inputs to optimize action understanding. In addition, M1 activation during action reading is also under debate, with certain researchers observing this activation (Aziz-Zadeh et al., 2006; Hauk

et al., 2004; Tettamanti et al., 2005) whereas others do not (de Zubicaray et al., 2013; Grossman et al., 2002; Longe et al., 2007; Wurm and Caramazza, 2019).

Several justifications are available regarding these discrepancies. The first concerns the type of analyses employed, stating that activity variations in M1 are “weaker” during motor imagery, action observation and action reading (compared to actual movement), making them more challenging to observe with whole brain analysis. For example, researchers reporting M1 activation during motor imagery have frequently employed an alternative analysis approach (Lotze et al., 1999; Porro et al., 1996; Sharma et al., 2008), whereby fMRI sensitivity on M1 is enhanced by performing small volume corrections on regions of interest. The second explanation emphasizes the very high spatial specificity of fMRI at the expense of temporal sensitivity. Indeed, changes in M1 may occur very prematurely with a high degree of temporal specificity, making them more difficult to detect with fMRI. To illustrate, Dechent et al. (2004) noticed only a transient involvement of M1 at the onset of the motor imagery. In addition to these two restricting factors, current fMRI technologies are not sensitive enough to inform about the nature of the changes, i.e., whether the activation concerns excitatory or inhibitory processes. One approach to overcome these limitations is to probe the involvement of M1 by means of the neuro-modulation techniques.

#### 2.2. Correlational evidence from transcranial magnetic stimulation studies

TMS is a non-invasive technique in which an electromagnetic field is delivered through a coil placed over the scalp. When the coil is placed over M1, one can elicit a motor-evoked potential (MEP) in the target muscles, measured with EMG electrodes. When a single-pulse TMS is triggered, the MEP amplitude provides a marker of corticospinal excitability at the time of stimulation. To note that each technique is constrained by a trade-off between temporal and spatial resolution (Walsh and Cowey, 2000). While fMRI allows the investigation of brain activity with a temporal resolution on the order of seconds, TMS enables the possibility to assess motor system activity (e.g., corticospinal excitability, intracortical facilitation and inhibition within M1, functional brain connectivity with M1) with a millisecond precision. This fine temporal resolution is particularly relevant for studying covert actions, specifically action reading: it allows the dissociation between an early functionally meaningful involvement of M1 in supporting lexico-semantic access (occurring between 200 ms and 400 ms), and a later post-conceptual activation emerging after 500 ms. Moreover, when a paired-pulse TMS is triggered, the modulation of MEP amplitude probes intracortical inhibition or facilitation within M1. This specific ability to quantify inhibitory and facilitatory mechanisms with high temporal resolution makes TMS a valuable neurophysiologic tool to investigate the involvement of fine-tuned neural structures within M1 during motor imagery, action observation and action reading.

##### 2.2.1. Motor imagery

Numerous studies have reported an increased corticospinal excitability during motor imagery, characterized by an increase in MEP amplitude while background EMG activity remained silent (Dupont et al., 2024b, 2023; Facchini et al., 2002; Fadiga et al., 1998; Grosprêtre et al., 2016a; Kasai et al., 1997; Lebon et al., 2012; Rossini et al., 1999; Tremblay et al., 2001). Interestingly, these brain-muscle excitability changes during motor imagery depend on somatotopic organization (Facchini et al., 2002; Marconi et al., 2007; Rossini et al., 1999; Tremblay et al., 2001), temporal factors (Fadiga et al., 1998; Hashimoto and Rothwell, 1999; Stinear and Byblow, 2003; Tatemoto et al., 2017), contextual aspects of the task (Fourkas et al., 2006; Mercier et al., 2008; Vargas et al., 2004) and the force intensity of the imagined action (Helm et al., 2015; Mizuguchi et al., 2013; for contradictory data, see Park and Li, 2011).

This suggests that the increase in corticospinal excitability is muscle-specific according to the imagined movement, and appears only if the stimulation is delivered during the active phase of movement imagination. For example, [Stinear and Byblow \(2004\)](#) reported that the MEP amplitude in hand muscles was significantly greater during the 'on' phase of imagined movement (where repetitive movements of the dominant index finger were paced by a 1 Hz auditory metronome), reflecting increased corticospinal excitability specifically when the movement was actively being imagined. This demonstrates the somatotopic and temporal influence of motor imagery on corticospinal excitability. Furthermore, the context and imagined strength level should also be taken into consideration in observations of corticospinal excitability increases. Indeed, the MEP facilitation of the hand muscles during imagined thumb abduction was greater when the hand was maintained in a task-compatible position compared to an incompatible one ([Vargas et al., 2004](#)). Also, a greater corticospinal excitability was observed for 60 % versus 10 % force level imagination ([Mizuguchi et al., 2013](#)).

Initially, this corticospinal excitability increase was attributed to a neuronal reactivity enhancement ([Fadiga et al., 1998](#); [Kasai et al., 1997](#); [Yahagi and Kasai, 1998](#)) and/or a decrease in intra-cortical inhibition ([Abbruzzese et al., 1999](#); [Kumru et al., 2008](#); [Liepert and Neveling, 2009](#); [Stinear and Byblow, 2004](#)). However, more recent research has reported no change ([Lebon et al., 2012](#); [Ridding and Rothwell, 1999](#)) or even an increase in short-interval intracortical inhibition within M1 during motor imagery, suggesting an inhibitory mechanism to prevent any potential motor output ([Neige et al., 2022, 2020](#)).

Overall, the evidence from TMS studies support the involvement of M1 during motor imagery with a specific increase in corticospinal excitability and modulations of intracortical neurons within M1.

### 2.2.2. Action observation

Similar to motor imagery, several studies showed an increase in corticospinal excitability when participants observed an action ([Aziz-Zadeh et al., 2002](#); [Borroni et al., 2005](#); [Brighina et al., 2000](#); [Clark et al., 2004](#); [Dupont et al., 2024b](#); [Fadiga et al., 2005, 1995](#); [Funase et al., 2007](#); [Gangitano et al., 2001](#); [Maeda et al., 2002](#); [Strafella and Paus, 2000](#)). As for motor imagery, somatotopic organization, stimulation timing, contextual factors, and the strength level of the observed movement may modulate such increases while observing actions.

[Naish et al. \(2014\)](#) suggested a model of corticospinal modulation during action observation in which somatotopic and temporal factors are integrated. First, approximately 80–150 ms after the visual perception of an action, there is an early and generalized corticospinal excitability increase ([Lepage et al., 2010](#)). Then, around 200–300ms, a later phase of corticospinal modulation is observed, with a greater increase for the muscle specifically involved in the observed movement ([Cavallo et al., 2014](#)). In addition, the contextual factor and the strength level of the observed movement also contribute to the modulation of corticospinal excitability. For instance, MEP facilitation during the observation of pinching objects was greater with a congruent context compared to an incongruent context ([Amoruso and Urgesi, 2016](#); [Riach et al., 2018](#)). Furthermore, several authors observed that object weight encoding was present during action observation, with higher MEP amplitude during the observation of heavy than light object lifting ([Alaerts et al., 2010, 2010](#); [Helm et al., 2015](#); [Senot et al., 2011](#)).

The increase in corticospinal excitability during action observation is mainly governed by certain modulations of activity in facilitatory or inhibitory interneuron networks. For example, [Strafella et al. \(2000\)](#) noted an increase in MEP amplitude associated with a decrease in intracortical inhibition when participants observed hand/arm movements. Other researchers have since replicated this result ([Cardellicchio et al., 2020, 2018](#); [Nuara et al., 2023](#); [Patuzzo et al., 2003](#)). However, when the observer has the intention to imitate the observed movement, a suppression mechanism might occur to counteract the increased excitability of motor pathways and prevent the immediate overt

imitation of observed actions ([Hardwick et al., 2012](#)). Overall, these contributions demonstrate an engagement of the corticospinal pathway and intracortical neurons within M1 during action observation.

### 2.2.3. Action reading

Similar to motor imagery and action observation, when single-pulse TMS is applied to M1 during action reading, the corticospinal excitability increases ([Dupont et al., 2024a, 2022](#); [Innocenti et al., 2014](#); [Labruna et al., 2011](#); [Papeo et al., 2009](#); [Scorolli et al., 2012](#); for review see, [Madden-Lombardi and Dupont, 2023](#)). For example, [Papeo et al. \(2009\)](#) reported an increase in corticospinal excitability only in the muscles involved in the described actions, and only at 500 ms, suggesting a role in post-conceptual processing. Other researchers observed such an increase, but at 300 ms, reflecting rather a lexical-semantic processing ([Innocenti et al., 2014](#); [Labruna et al., 2011](#)). In our view, modulations in the corticospinal pathway during action reading occur at different latencies for different individuals (typically between 200 and 500 ms). Given the fact that reading and decoding speed can vary greatly across individuals, we can imagine that the moment when the TMS pulse elicits the greatest MEP amplitude will vary depending on when lexical/semantic access and motor simulation occur ([Dupont et al., 2025a, b,c](#)).

However, to our knowledge, TMS research on action reading regarding contextual and/or action intensity effects remains limited ([Dupont et al., 2022](#)). Nevertheless, it seems highly plausible that MEP amplitude would be modulated in accordance with the context or action intensity in the sentence, as fMRI and behavioral studies have already reported such effects ([Beauprez et al., 2018](#); [Gilead et al., 2013](#); [Kemperer, 2015](#); [Papeo et al., 2012](#); [Raposo et al., 2009](#); [Van Dam et al., 2014, 2012, 2010](#)). Despite the limited TMS data on these later factors, we can suggest that as in motor imagery and action observation, changes in the corticospinal pathway excitability during action reading would likely be sensitive to somatotopic, temporal, and contextual aspects, as well as the force intensity conveyed by action sentences.

The current literature on facilitatory and inhibitory processes that might explain corticospinal modulations during action reading is rather sparse. A study by [Onmyoji et al. \(2015\)](#) noted that reading action sentences aloud elicited greater corticospinal excitability with no observed change in short-interval intracortical inhibition (paired-pulse TMS), suggesting an increase in facilitatory rather than a decrease in inhibitory mechanisms. Nevertheless, reading aloud engages articulatory movements, which can influence facilitating and inhibiting neural networks in ways that differ from silent reading. Recently, ([Dupont et al., 2025a,b,c](#)) examined the modulation of short-interval intracortical inhibition at early (between 200 ms and 500 ms) and late (700 ms and 900 ms) latencies during silent reading of action sentences. Interestingly, they observed an increased intracortical inhibition only at later latencies, which may reflect a mechanism to counter motor facilitation and prevent actual movement. While further experimental contributions are required to draw clear conclusions about the involvement of inhibitory and facilitatory mechanisms within M1 during action reading, TMS findings generally support the idea that the motor system is engaged during the comprehension of action verbs.

## 2.3. Correlational evidence from aphantasia

Finally, a deeper and more comprehensive understanding can be gained by examining the relationship between aphantasia — defined as an impairment or inability to perform voluntary mental imagery ([Zeman et al., 2015](#)) — and the recruitment of the motor system during imagining, observing, or reading actions. Interestingly, aphantasia has recently attracted significant attention in the scientific community due to its unique characteristics. Traditionally, this primarily congenital and otherwise healthy cognitive profile has been evaluated through subjective scores of the visual imagery vividness (Vividness of Visual Imagery Questionnaire - VVIQ, see [Dance et al., 2022](#); [Zeman et al., 2020](#)) or

behavioural paradigms such as binocular rivalry (Keogh and Pearson, 2021, 2018). These reports consistently suggest that individuals with aphantasia struggle to generate mental simulations or are entirely unable to do so (Keogh and Pearson, 2018; Zeman et al., 2020, 2015). Zeman et al. (2015) reported that 21 individuals (who had contacted them) mentioned difficulties or an inability to generate visual imagery, with 10 of them also experiencing impairments across other imagery modalities. Additionally, a recent physiological study indicates that this deficit is not merely a matter of strategy or metacognitive control (Kay et al., 2022). By studying individuals with aphantasia, we can gain valuable insights into the essential roles of motor simulations in these cognitive functions supported by the recruitment of the motor system. Nonetheless, the neurophysiological evidence available to date primarily concerns brain activation during mental or visual imagery (Liu et al., 2025; Milton et al., 2021), and no study used fMRI (or other relevant techniques) to investigate the potential differences in brain activations during motor imagery, action observation, or action reading in these individuals.

Employing TMS, Dupont et al. (2024a, 2024b) recently provided neurophysiological and objective evidence demonstrating that aphantasic individuals failed to recruit the motor system during both explicit and implicit forms of mental simulation of movements. In these studies, individuals with aphantasia (impaired imagery) or not (normal imagery) were asked to imagine, observe and read actions describing a pinch movement between the thumb and pointer finger. While participants were engaged in these tasks, single-pulse TMS was delivered over the left M1 (finger area of the right hand). Individuals with normal imagery ability typically exhibited an increase in corticospinal excitability during motor imagery, action observation and action reading. However, those with aphantasia did not show such modulations. As supported by (Tomasino et al., 2007, 2008; Tomasino and Rumiati, 2013, participants activating the motor system are those employing a motor simulation during action reading, and conversely, participants not engaging this motor simulation fail to elicit such motor activation. Furthermore, the absence of motor simulations and motor system activation during reading results in an impaired deep-level reading comprehension ability, characterized by a difficulty in selecting words that best fit the context of sentences (Dupont et al., 2024a). These groundbreaking results have once again demonstrated a valuable contribution of motor simulations and motor system activation for action reading. Thus, although the M1 is not the central component for imagining or understanding actions, its activation plays a role in optimizing these processes.

#### 2.4. Conclusions based on correlative evidence

Taken together, correlational evidence, notably provided by fMRI or PET studies, suggests that motor imagery, action observation, and action reading engage (at least) a broad fronto-parietal network, comprising the motor system and especially M1. The fine temporal resolution of TMS further indicates that the activation of motor system, particularly in M1, occurs at an early stage (between 200 and 400 ms). This temporal dynamic is consistent with previous EEG and MEG evidence and suggests a potential functional contribution of the motor system to imagining and understanding actions (Hauk and Pulvermüller, 2004; Pulvermüller et al., 2005, 2000). However, it is important to note that a correlational approach cannot establish whether neural activity in motor regions contributes in a meaningful way, or what exact role it plays, to our cognitive experience of imagining, observing, or reading about actions. In fact, correlational data only reveal that certain brain networks are activated during these tasks, without demonstrating whether this activation is necessary or directly contributes to imagining or understanding actions.

### 3. Causal evidence

We believe that exploring causal evidence is crucial to establishing a

clear link between brain structures and their associated functions. Thus, to substantiate the conclusions drawn in the correlational sections, it is essential to consider data derived from studies focusing on behavioral changes, patients with lesions, and artificial lesions induced by neuro-modulation techniques in healthy participants. First, the forthcoming section will provide information about the relationship between motor impairments or lesions in the motor cortex and their impact on motor imagery, action observation, and action reading comprehension abilities. Second, we will discuss scientific findings that investigate the causal role of the motor system in these processes by deliberately disrupting the motor cortex through non-invasive brain stimulation techniques such as transcranial direct current stimulation (tDCS) or repetitive transcranial magnetic stimulation (rTMS). Finally, we will examine bidirectional influences between these three processes and actual movement, which will enhance our understanding of covert actions.

#### 3.1. Causal evidence from motor system disorders

##### 3.1.1. Motor imagery and motor system impairment

Motor lesions refer to damage or disruption in specific regions of the motor system, including the motor cortex and related areas, which can significantly affect motor functions, such as planning, control or execution of movements. Over the past several decades, research has shed new light on the impact of motor cortex lesions on motor imagery abilities. In a pivotal study by Sirigu et al. (1995), a patient living with a lesion to M1 and disruptions of motor behavior was asked to either physically perform or imagine arm-pointing movements. Interestingly, this lesion led to significantly reduced performance in both actual and imagined conditions, characterized by increased movement durations. More recently, in a systematic review, McInnes et al. (2016) summarized results from 10 patients with lesions located within M1. Among these patients, six showed no motor imagery impairment and four exhibited a reduced ability, but none of them exhibited a complete inability to imagine movements. These results suggest that isolated M1 lesions may impair but not prevent motor imagery. However, when lesions affected other parts of the motor system, such as the premotor areas, the impact on motor imagery was particularly detrimental, highlighting the crucial role of this motor area for motor imagery (McInnes et al., 2016; Oostra et al., 2015). Furthermore, additional evidence comes from studies revealing a strong relationship between motor impairments and deficits in motor imagery. For instance, Dettmers et al. (2012) revealed that the severity of motor impairment after a stroke affected motor imagery ability, with patients suffering from severe motor trouble (paresis) scoring lower on motor imagery questionnaires than those with moderate motor trouble. Similarly, Williams et al. (2008) observed that children with developmental coordination disorders displayed varying degrees of motor imagery impairment, with severe cases showing more pronounced motor imagery deficits than moderate cases. Taken together, lesion studies suggest that the motor system in general plays a crucial role in motor imagery while M1 contributes to optimizing motor simulations.

##### 3.1.2. Action observation and motor system impairment

Similar to motor imagery, recent research has explored the impact of motor system impairment on action observation and recognition abilities. Initial cases involved patients with motor disorders such as apraxia or hemiplegia. For instance, patients living with apraxia (impairment in high-level motor planning) exhibited deficits not only in action execution, but also in recognition of biological movement, linked to lesions in the fronto-parietal regions and especially the inferior frontal gyrus (Pazzaglia et al., 2008a, 2008b). Interestingly, patients with hemiplegia showed preserved action recognition when viewing actions involving their unaffected arm but their performance was impaired when the observed actions involved their hemiplegic arm (Serino et al., 2010). Patients with spinal cord injury, characterized by the non-use of body

parts following deafferentation, also showed impaired recognition of biological movement (Arrighi et al., 2011; Pernigo et al., 2012). Taken together, these findings suggest a link between impairment of the motor system and deficits in action recognition. However, the literature also presents some contradictions. For instance, some studies indicate that patients with brain lesions within motor areas present difficulty performing actions in the absence of any deficit in action recognition (Negri et al., 2007; Stassenko et al., 2013; Vannuscorps and Caramazza, 2016). Overall, while certain findings highlight a potential role of the motor system in action recognition, further research is necessary to clarify divergences in the literature.

### 3.1.3. Action reading and motor system impairment

In parallel to motor imagery and action observation, language studies have also investigated the causal role of the motor system in understanding described actions. If lesions in the motor system result in a deficit or inability to comprehend action words, the engagement of motor areas (notably M1) cannot be considered merely epiphenomenal during reading comprehension. Two patients with lesions in the supplementary motor or primary motor areas performed a lexical decision task involving action-related object names (Dreyer et al., 2015). Interestingly, such lesions resulted in diminished comprehension of action words, a finding corroborated by follow-up research (Dreyer et al., 2020). These results from patients with motor system lesions are consistent with earlier studies illustrating that patients with broader motor system impairments manifest specific deficits in processing motor-related words (Daniele et al., 1994; Grossman et al., 2008; Neiningner and Pulvermüller, 2003; Riccardi et al., 2020). Together, these contributions bolster the notion that activation of the motor system contributes to the comprehension of action words.

### 3.1.4. Motor system lesions: what can we learn from them?

The previous sections have reviewed evidence regarding the contributing role of the motor system in motor imagery, action observation and action reading. Nonetheless, the findings are not always straightforward, and several factors may explain these discrepancies. First, patient data show considerable variability, primarily caused by significant differences in lesion sites. Of course, researchers cannot control the precise location of the lesions, making it difficult to ensure their homogeneity within or across studies. Second, both motor imagery and understanding an action during observation or reading require a broad network rather than an isolated area. An isolated lesion in the network may not systematically result in a complete loss of functionality. To illustrate, even though impairments in movement recognition have been associated with parietal cortex lesions, particularly in the inferior parietal lobule alone (Buxbaum et al., 2005; Urgesi et al., 2014), some studies suggest that it is rather an association with lesions in the inferior frontal gyrus (Pazzaglia et al., 2008b; Tranel et al., 2008) or temporal gyrus (Buxbaum et al., 2014; Urgesi et al., 2014), which yields these deficits. Thus, lesions in both the inferior frontal gyrus and the parietal lobe may be necessary to observe a real impairment in movement comprehension (Binder et al., 2017; Freund, 2003; Halsband et al., 2001). This idea suggests that a lesion in M1 can impact overt action, but might not necessarily lead to a deficit or inability in covert actions unless it is accompanied by damage to another critical area involved in imagining, observing or reading actions. Finally, it is very common for patients to have lesions in multiple areas, compromising the possibility to accurately infer the specific role and importance of the targeted brain region.

## 3.2. Causal evidence from virtual disruption of the motor system

To overcome the limitations of patient-based studies as described above, some studies employ neuromodulation techniques that temporarily disrupt a certain brain area, as if it were damaged by a lesion, but only for the duration of the experiment. This "virtual lesion", by means of

tDCS or rTMS, can transiently disrupt the function of a targeted brain area, depending on the duration, intensity, and frequency of the stimulation protocol (Huang et al., 2005; Klomjai et al., 2015; Sudbrack-Oliveira et al., 2021).

### 3.2.1. Motor system neuromodulation during motor imagery

Using neuromodulation techniques, researchers have frequently reported that disruptive or facilitative transcranial stimulation targeting the motor cortex impacts motor learning acquired through motor imagery practice (Date et al., 2015; Debarnot et al., 2019, 2011; Foerster et al., 2013; Matsumoto et al., 2010; Saimpont et al., 2016; Saruco et al., 2017). For instance, Saimpont et al. (2016) observed that motor imagery coupled with anodal (facilitative) tDCS over M1 improved performance after motor imagery practice to a greater extent than motor imagery alone. Debarnot et al. (2011) illustrated that applying inhibitory rTMS over M1 immediately after motor imagery practice abolished the initial performance boost, highlighting the crucial role of M1 in mediating early gains in performance induced by motor imagery. On the contrary, Kraeutner et al. (2017) did not find any significant differences in motor-imagery-based motor learning, using the same inhibitory rTMS protocol over M1. Thus, while most studies demonstrate the involvement of M1 in optimizing the motor learning process acquired with motor imagery, some discrepancies persist. These variations could be partially attributed to experimental parameters, such as the number of stimulation sessions, the stimulation parameters or the nature of the motor imagery task. For instance, a recent study suggested that multiple sessions of tDCS was more effective in bolstering the effects of motor training compared to a single session (Hashemirad et al., 2016). Consequently, further tDCS and rTMS investigation is warranted to support the contributing role of M1 in motor imagery and mental-based motor learning.

### 3.2.2. Motor system neuromodulation during action observation

Similar to motor imagery, studies have investigated whether disruptive or facilitative transcranial stimulation targeting M1 also influences action observation (Naish et al., 2016; Palmer et al., 2016; Paracampo et al., 2018). For instance, Palmer et al. (2016) tested the possible causal role of M1 in interpreting visually presented actions with inhibitory rTMS over left M1. They found a decreased sensitivity in individuals to infer the kinematics of observed actions following M1 disruption. Furthermore, there was a significant positive correlation between the magnitude of motor excitability suppression and participants' performance. This notion was further corroborated by Naish et al. (2016), who demonstrated that disrupting M1 with subthreshold single-pulse TMS impaired the recognition of observed actions. Also, Paracampo et al. (2018) showed that disruptive (cathodal) tDCS over left M1 just before the task impaired the prediction accuracy of observed reach-grasp movements. Whether using rTMS or tDCS, these results support the functional role of M1 in recognizing and predicting outcomes of observed actions.

### 3.2.3. Motor system neuromodulation during action reading

Researchers investigated whether a disturbance of M1 using rTMS or tDCS impacted the comprehension of action words. For instance, Repetto et al. (2013) administered inhibitory rTMS over the hand motor area of M1 during a lexical decision task involving words referring to actions or abstract concepts. Here, the authors observed slower reaction times for action verbs following disruptive stimulations, but no difference for abstract verbs. This finding was corroborated by other rTMS and high-definition tDCS investigations, suggesting that the motor cortex contributes to the processing of semantic representations of action words, and not the representation of grammatical concepts (Gerfo et al., 2008; Johari et al., 2022; Vukovic et al., 2017). Taken together, while comprehension may be diminished, or less efficient following the disruption of M1, it is not completely blocked. The current findings suggest that M1 plays a role in optimizing this process, refining linguistic

comprehension, and rendering it more efficient when necessary.

### 3.3. Causal evidence from behavioral studies

In this final section, we will explore the bidirectional influences between actual movements and motor imagery, action observation, and action reading. Specifically, we will examine how these three covert actions impact various behavioral parameters, such as strength and speed-accuracy tasks. Additionally, we will investigate how behavioral tasks, in turn, influence the execution and the effectiveness of these covert actions.

#### 3.3.1. The bi-directional influence of motor imagery and movement

Among early studies that truly focused on motor imagery and performance, several investigated the strength modulations resulting from motor imagery training (Ranganathan et al., 2004; Yue and Cole, 1992). For example, Yue and Cole (1992) demonstrated that imagining hand movements increased manual strength. This ground-breaking study has been replicated extensively for the imagination of hand/arm movements (Di Rienzo et al., 2015; Ranganathan et al., 2004; Smith et al., 2003), and extended to lower limb strength (Cornwall et al., 1991; Grosprêtre et al., 2018; Lebon et al., 2010; Reiser et al., 2011; Sidaway and Trzaska, 2005; Zijdewind et al., 2003). As several studies reported no morphological adaptations (muscle increase) after motor imagery training, this strength increase is presumed to arise from neural origins. Nevertheless, it should be mentioned that some researchers failed to observe a significant increase in strength after motor imagery training (de Ruyter et al., 2012; Herbert et al., 1998; Manocchio et al., 2015).

Researchers have also reported an impact of motor imagery training on other performance parameters, such as speed-accuracy trade-off, i.e., pointing, arm reaching or tapping movements as quickly and accurately as possible (Allami et al., 2008; Gentili et al., 2010, 2006; Gentili and Papaxanthis, 2015; Pascual-Leone et al., 1995; Ruffino et al., 2022, 2021; Yáñez et al., 1998). For example, Gentili et al. (2015) observed that both physical and motor imagery practice decreased movement duration during successive reaching movements. This improvement during pointing or arm reaching tasks is hypothesized to stem from the updating of sensorimotor representations in the absence of movement. This suggests that motor imagery may be able to improve motor performance, which could have consequential applications in the domain of athletic performance as well as physical rehabilitation (Ladda et al., 2021; Malouin and Richards, 2010).

In addition to these effects from focused sessions of motor imagery training, an influence of motor imagery on subsequent movement has also been observed, elucidating the interference or facilitation of motor imagery on movement initiation (Li et al., 2009; Ramsey et al., 2010; Toovey et al., 2021). For example, in the study of Ramsey et al. (2010), participants grasped an object following congruent or incongruent motor imagery. In their first experiment, movement initiation was faster following congruent compared to incongruent imagery, demonstrating that imagery can prime the initiation of grasping. In a second experiment, incongruent imagery resulted in slower movement initiation compared to a no-imagery control, suggesting that the congruence effect may be, at least partially, the result of interference from imagining a different action than the one to be performed. Taken together, these data show that imagining can facilitate and interfere with action production.

Moreover, although the reverse effect is less frequently reported, it appears that incorporating actual movements can improve the effectiveness of motor imagery on motor performance (Fusco et al., 2018; Gould et al., 2013; Guillot et al., 2013). For instance, Guillot et al. (2013) investigated whether incorporating actual movement execution during motor imagery (i.e., a dynamic imagery condition) would enhance motor performance more effectively than motor imagery alone. Their findings indicated that physically executing the movement during motor imagery not only improved the quality of the motor imagery itself but also resulted in greater performance gains afterward. This idea is

consistent with theoretical models on motor imagery and performance (e.g., Holmes and Collins, 2001) and was corroborated by several more recent studies aiming to increase the effectiveness of motor imagery (Fusco et al., 2018; Gould et al., 2013). Taken together, these findings suggest a bi-directional influence of motor imagery and movement.

#### 3.3.2. Bi-directional influence of action observation and movement

Similar to motor imagery, several studies demonstrated the impact of action observation on performance in sports and physical rehabilitation (Rannaud Monany et al., 2022b). The influence of action observation has been reported on various types of physical performance, such as increases in strength (Di Rienzo et al., 2019; Losana-Ferrer et al., 2018; Porro et al., 2007), aerobic performance (Wrightson et al., 2016) and technical motion in golf (Kim et al., 2017). For example, Di Rienzo et al. (2019) demonstrated that action observation training of elbow flexion increased the maximal strength of this action. This strength gain after action observation training is not generated by muscular modifications, but rather by neural modulations.

Additionally, action observation has been shown to affect the execution of subsequent movements in terms of speed, accuracy and hand aperture during pointing, reaching and grasping movements (Brass et al., 2001, 2000; Castiello et al., 2002; Craighero et al., 1997; Dijkerman and Smit, 2007; Edwards et al., 2003; Gianelli et al., 2008; Griffiths and Tipper, 2009; Hardwick and Edwards, 2012, 2011; Kilner et al., 2003; Ménoret et al., 2013; Salama et al., 2011). For example, Ménoret et al. (2013) asked participants to grasp an object composed of a large and a small part, and measured how kinematic parameters (including the transport and grasping components) were affected by movement observation. They reported facilitation of the transport and grasp components characterized by an increase in velocity peak. However, this performance enhancement depends on the temporal course between observation and the subsequent action (Ménoret et al., 2013), as well as the compatibility between the observed and executed actions (Kilner et al., 2003). Based on these findings, it appears that action observation may influence physical performance, including strength and kinematic parameters.

As seen in motor imagery, action observation also appears to be influenced by motor training (Beets et al., 2010; Casile and Giese, 2006; Hecht et al., 2001; for review see: Schütz-Bosbach and Prinz, 2007). For instance, Casile et al. (2006) asked participants to visually recognize gait patterns before and after motor training, and reported that movements influenced visual action perception. They postulated that motor training might induce modulations in somatosensory activation patterns that were unconsciously triggered during visual recognition, and could facilitate action understanding. Interestingly, this motor influence on an action observation task was also reported when the two tasks were performed subsequently (Craighero et al., 2002). As we have already seen for motor imagery, these findings suggest a bi-directional influence of action observation and movement.

#### 3.3.3. Bi-directional influence of action reading and movement

Action reading has been shown to increase various aspects of physical performance, such as response time (Andres et al., 2015; Klepp et al., 2019; Taylor and Zwaan, 2008), reaching and grasping movements (Gentilucci et al., 2000; Gentilucci and Gangitano, 1998; Glenberg and Kaschak, 2002; Glover and Dixon, 2002; Kaschak and Borreggine, 2008) and strength during complex (Rabahi et al., 2013, 2012) or isometric movements (Frak et al., 2010). For example, Rabahi et al. (2013) reported that reading action verbs like “jump” increased the height of a squat jump. This finding was corroborated by Frak et al. (2010), showing an increase in grip force during the reading of manual action verbs. Such enhancement may result from motor output facilitation during the motor simulation of the action verb.

Additionally, the comprehension of action verbs may impact subsequent reaching and grasping movements (Gentilucci, 2003, 2002; Gentilucci et al., 2000; Glover et al., 2004; Glover and Dixon, 2002). For

instance, Gentilucci et al. (2000) asked participants to reach and grasp an object imprinted with words such as "near/far" or "small/large." They revealed that the kinematics of reaching-grasping were affected by the meaning of the printed words. Specifically, it appears that the inclusion or modification of object properties related to sensorimotor processing may automatically affect the object-related motor representation and consequently, the subsequent movement. However, this facilitation effect is only present if the linguistic content is compatible with the motor task and is presented at a specific moment, this is called the "action compatibility effect" (Dalla Volta et al., 2009; Gentilucci et al., 2000; Glenberg and Gallese, 2012; Taylor and Zwaan, 2008; Van Dam and Desai, 2017; Zwaan et al., 2012; for contradictory views see: Morey et al., 2022; Papesch, 2015).

The reverse effect has also been investigated, that is, the potential influence of movement on action reading. In particular, motor preparation and execution have been shown to exert an influence on action understanding and representations (Rueschemeyer et al., 2010; van Dam et al., 2013, 2010; Van Elk et al., 2008; Yang, 2014). For example, Rueschemeyer et al. (2010) asked participants to execute index finger movements while engaging in a lexical decision task on words about manipulable or non-manipulable objects. Lexical decisions for manipulable object words were facilitated, suggesting that movement execution may influence action reading. Moreover, Van dam et al. (2013) used a go/no-go lexical decision task to demonstrate that utilizing an object to prepare congruent actions facilitates processing of the word denoting the object. Furthermore, action reading understanding is influenced by the repetition of a movement during motor training (Glenberg et al., 2008; Locatelli et al., 2012; Trevisan et al., 2017). For example, Locatelli et al. (2012) reported that three weeks of manual action training led to enhancements in a semantic language task. The authors suggested that gains in sensorimotor expertise during manual training may lead to improved semantic processing skills during action reading, an effect that depends on the trained actions. These results demonstrate that motor training can influence sensorimotor representations during action reading and consequently, its understanding. Taken together, these findings suggest a bi-directional influence of action reading and movement.

### 3.3.4. Motor imagery, action observation and action reading to improve motor learning and rehabilitation

In the previous sections, we highlighted that motor imagery, action observation and action reading offer the promising potential to further optimize motor performance. Notably, several researchers propose that covert action-based interventions are precursors to physical therapies, facilitating early motor rehabilitation in cases where physical neuro-rehabilitation would otherwise be impractical. Additionally, when combined with traditional sports or rehabilitation programs, such interventions can increase the overall training dosage and thereby further optimize motor training outcomes (for reviews, see Rizzolatti et al., 2021; Ruffino et al., 2017). Indeed, covert actions — particularly motor imagery or action observation — can reinforce motor learning in healthy individuals, and even among high-level athletes (Bird et al., 2005; Gatti et al., 2013; Guillot et al., 2009a,b; Mattar and Gribble, 2005; Ruffino et al., 2022, for review, see Ruffino et al., 2021). Likewise, an increasing body of research supports the use of covert actions to improve altered motor functions in individuals living with various motor disabilities, e. g., stroke (Borges et al., 2022; Liu et al., 2004; Tani et al., 2018; Tong et al., 2017; Villa-Berges et al., 2023), or hypoactivity (Bassolino et al., 2014; Clark et al., 2014; De Marco et al., 2021; Debarnot et al., 2021; Newsom et al., 2003; Stenekes et al., 2009).

Interestingly, a compelling approach consists of combining two forms of covert action, such as action observation and motor imagery, referred to as AOMI intervention (Wright et al., 2022) or Action Observation Training, which effectively combines action observation, motor imagery, and action execution (Rizzolatti et al., 2021). As such, this provides an opportunity to further increase motor system activity

(Eaves et al., 2016; Nedelko et al., 2012; Taube et al., 2015; Wright et al., 2014), thereby leading to greater improvements in motor function across both sport and clinical applications (Binks et al., 2023; for reviews see, Eaves et al., 2024, 2016; Rannaud Monany et al., 2022b; Vogt et al., 2013). These findings suggest that engaging in at least two covert action processes simultaneously may bolster the motor system activity and the brain plasticity beyond what is achieved through isolated motor imagery or action observation. Nevertheless, for such intervention, some recommendations are provided, such as congruence between the observed and imagined action, or the personalization of the motor imagery component (Rannaud Monany et al., 2022b; Wright et al., 2022). The identification of a commonly activated motor network, potentially playing a functional role for imagining and understanding actions, opens up the possibility of combining covert actions to enhance motor performance in both sport and clinical contexts. However, it is worth noting that the literature has not yet explored potential combinations involving action reading (for review on motor imagery and action language, see Bayram et al., 2023).

## 4. Futures directions

The current review points out that the motor system, including M1, is clearly engaged during motor imagery, action observation and action reading. Despite the promising correlational and causal evidence available in the literature, some questions remain and need to be addressed to fully understand the functional role of M1 in the covert actions.

First, corticospinal excitability should not be interpreted solely as a direct reflection of local activity within M1, but rather as the capacity of specific cortical neurons — notably located in the posterior regions of the frontal and parietal lobes — to project to the spinal cord before establishing connections with peripheral motoneurons. As studies involving macaques and rats have demonstrated that corticospinal projections from M1 are particularly abundant and exert a highly facilitatory influence (Dum and Strick, 1991; He et al., 1995, 1993; Maier et al., 2002; Miller, 1987), such increased corticospinal excitability during motor imagery, action observation and action reading could likely be associated with M1 activity. Nonetheless, it may also reflect facilitatory inputs originating in regions interconnected with M1 (Nuara et al., 2023, for reviews see, Derosiére and Duque, 2020; Reis et al., 2008). Indeed, other cortical regions contribute to these corticospinal projections, such as the premotor cortex (Buch et al., 2010; Civardi et al., 2001; Davare et al., 2009; Dum and Strick, 1991; He et al., 1993), the supplementary motor area (Civardi et al., 2001; He et al., 1995; Maier et al., 2002), the anterior intraparietal sulcus (Allart et al., 2019; Vesia et al., 2013), the superior parietal lobule (Mackenzie et al., 2016) and the supramarginal gyrus (Koch et al., 2010). Therefore, further research should aim to clarify its precise origins, particularly using double-coil TMS or the coupling TMS-EEG, which is currently lacking in the field of covert actions.

Second, it is essential to emphasize that, regardless of its origin or functional contribution, the modulation of motor system activity in response to motor imagery, action observation, and action reading exhibits substantial interindividual variability. For example, recent TMS studies have shown that between 23 % and 34 % of individuals displayed no increase — or even a decrease — in corticospinal excitability during motor imagery (Dupont et al., 2024b), action observation (Dupont et al., 2024b; Nuara et al., 2023) and action reading (Dupont et al., 2024a). In a similar vein, some studies using fMRI or EEG reported the same interindividual variability phenomenon during motor imagery (Dupont et al., 2025b; Höller et al., 2013; Leonardo et al., 1995; Nair et al., 2003; Roth et al., 1996; Wriessnegger et al., 2020). One potential factor that may explain this variability is the anatomical and functional heterogeneity of M1 itself. Indeed, recent studies suggest that M1 comprises several subdivisions that contribute to two distinct neural systems: one that is purely motor, involved in effector-specific

movement during fine motor control, and another that could be considered as somato-cognitive, involved in integrating motor actions with goals, physiological states, and body awareness (Gordon et al., 2023; Jensen et al., 2023). In the context of covert actions, the subdivisions of M1 appear to be differentially engaged. For instance, although overall M1 activity during motor imagery is weaker than during motor execution (Lotze et al., 1999; Miller et al., 2010; Sharma et al., 2008), one subdivision (area 4p) exhibits distributed activation that is both stronger and more closely aligned with motor execution than that observed in another subdivision, namely area 4a (Sharma et al., 2008). Therefore, these findings highlight the need for future research to disentangle the specific functional contributions of each M1 subdivision.

## 5. Discussion and conclusion

Many brain regions associated with the motor system — such as M1, the supplementary motor area, the premotor cortex and the parietal cortex — are consistently activated during motor imagery, action observation and action reading. According to the current literature, the parietal cortex is thought to contribute to the generation of motor representations, whereas the premotor cortex is frequently associated with the planning and preparation of these motor processes (Guillot et al., 2014; Hardwick et al., 2018). In contrast, the specific contribution of other regions, such as M1 and the dorsolateral prefrontal cortex (dlPFC), is still a matter of debate. For instance, the dlPFC might play the role of a functional hub for “motor working memory” supporting the generation of the action simulation (Jeannerod, 2001; Van Caenegem et al., 2024). Regarding M1, some researchers suggested that it might be part of a distributed network, including the parietal lobe, the premotor cortex and the cerebellum. This network would facilitate actual motor learning by storing or modifying the representation of action map (Penhune and Doyon, 2005; Penhune and Steele, 2012). Building on this evidence, one might hypothesize that a comparable mechanism could operate during covert actions, with M1 as a part of this distributed network, contributing to the storage of motor representations that would be retrieved in order to imagine or understand an action. Nevertheless, other researchers suggest that M1 might contribute to other functions, such as encoding directional information of the imagined or observed movements (Sharma et al., 2008). Importantly, given that patients with lesions located within M1 exhibit impaired, but not abolished, motor imagery or action comprehension (Dreyer et al., 2015; McInnes et al., 2016), M1 might act as a crossroads between multiple cortical regions and as a gateway to spinal structures (see Dupont et al., 2025a,b,c; Grosprêtre et al., 2019, 2016 for spinal activation during covert actions). Taken together, these findings indicate that covert actions should not be regarded only as cognitive processes, but also as motor processes.

To conclude, the current narrative review supports the involvement and functional role of the motor system — notably M1 — in both imagining and understanding actions, whether through action observation or action reading. The correlational and causal evidence presented in this review argues in favor of a dynamic embodiment mechanism that optimizes the imagination and comprehension of actions, rather than reflecting a mere epiphenomenon. These insights not only deepen our understanding of brain function and human cognition, but also hold promising practical implications for enhancing motor performance in both athletic and clinical contexts by means of covert actions.

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The author has no competing interests to declare.

## Data availability

No data was used for the research described in the article.

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